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Protelenomus Kieffer is a derived lineage of *Trissolcus* Ashmead (Hymenoptera, Scelionidae), with comments on the evolution of phoresy in Scelionidae

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Abstract

Species of the genus *Protelenomus* Kieffer (Platygastroidea, Scelionidae) are phoretic egg parasitoids of coreid bugs. The discovery, DNA sequencing, and molecular phylogenetic analysis of a *Protelenomus* species phoretic on *Cletus punctiger* (Dallas) (Hemiptera, Coreidae) shows that *Protelenomus* is a derived lineage of *Trissolcus* Ashmead. *Protelenomus* is treated as a junior synonym and a new species of phoretic *Trissolcus*, *T. siliangae* Yan, Chen & Talamas, is described from China.

Keywords

Coreidae, egg parasitoid, Hemiptera, integrated taxonomy, phylogenetics

Introduction

Scelionid parasitoids of hemipteran eggs are the subject of active study, driven by the economic damage caused by a variety of bug pests, and by recent works that accelerate further advancement. These include progress in the taxonomy and systematics of these parasitoids, which underlie accurate identification and classification (Talamas et al. 2017; Talamas et al. 2019; Tortorici et al. 2019; Talamas et al. 2021). *Protelenomus*

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Kieffer, a genus of egg parasitoids that are phoretic on Coreidae, was recently revised by Veenakumari et al. (2019), who described six new species, tripling the size of the genus. This treatment significantly expanded the known diversity of *Protelenomus* and brought attention to its uncertain generic status. Presently, *Protelenomus* cannot be unambiguously separated from *Trissolcus* Ashmead. Indeed, all of the characters used to define *Protelenomus* can be found in *Trissolcus*: T2 is longer than wide in *T. ancon* Johnson (Johnson 1991), *T. hyalinipennis* Rajmohana & Narendran has 4 clavomeres (Talamas et al. 2017), facial striae are found on species from both North America and Asia (Talamas et al. 2015; Talamas et al. 2017), and notauli are absent in many species (Johnson 1985; Talamas et al. 2017). In addition, *Trissolcus* species exhibit a wide range of sculpture on the frons, from coarsely rugose (*T. painei* (Ferrière)) to mostly smooth and shining (*T. perepelovi* (Kozlov)).

Even modification of the legs, which is pronounced in some species (e.g., *P. tibialis* Veenakumari), is not ubiquitous in *Protelenomus*. Given the nebulous boundary between *Protelenomus* and *Trissolcus*, we investigated the possibility that *Protelenomus* is a lineage derived from within *Trissolcus*, an idea first proposed by Masner (1976). The acquisition of freshly collected specimens, phoretic on Coreidae in China, combined with data made available by Talamas et al. (2019) and Vasiliţa et al. (2021), provided the opportunity to determine the placement of *Protelenomus* using molecular analysis.

Materials and methods

During a survey of insect pests and their parasitoids in a corn field in Wenzhou, Zhejiang Province, China, in the autumn of 2021, four female coreid bugs were found to each harbor a phoretic wasp dorsally on the head near the base of the antennae Fig. 1. Both the host and wasp specimens were collected and preserved in 100% ethanol until further study. The coreids were identified as *Cletus punctiger* (Dallas) using the key and description by Gupta and Singh (2013). All specimens are deposited in the Insect Collection of South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (**SCBG**) and the Insect Collection of Wenzhou Vocational College of Science and Technology, Wenzhou, China (**WVCST**).

Morphological terms

Abbreviations and morphological terms used in text: **A1**, **A2**, ... **A12**: antennomere 1, 2, … 12; **OOL**: ocellar-ocular length; **POL**: posterior ocellar length; **OD:** ocellar diameter; **T1**, **T2**, ... **T7**: metasomal tergite 1, 2, ... 7; **S1**, **S2**, ... **S7**: metasomal sternite 1, 2, … 7. Morphological terminology otherwise generally follows Mikó et al. (2007), Talamas et al. (2017), and Tortorici et al. (2019).

Character annotations

sasu subacropleural sulcus (Fig. 4B);
mtnm metanotum (Figs 4A, 5B);
mtpm metapostnotum (Figs 4A, 5B);
pl parapsidal line (Fig. 5A, B);
ppm propodeum (Figs 4A, 5B).

Molecular analysis

Genomic DNA was extracted using a TIANamp Micro DNA Kit (Tiangen Biotech (Beijing), Co.., Ltd), following the nondestructive DNA extraction protocol described in Taekul et al. (2014). Four molecular markers were amplified: two nuclear ribosomal (18S and 28S D2-3), one mitochondrial protein (COI), and one single-copy nuclear protein (wingless). Polymerase chain reactions were performed using Tks Gflex DNA Polymerase (Takara) with primer pairs shown in Table 1 and conducted in a T100 Thermal Cycler (Bio-Rad). Thermocycling conditions consisted of an initial denaturing step at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s and an additional extension at 72 °C for 5 min. Amplicons were directly sequenced in both directions with forward and reverse primers on an Applied Biosystems (ABI) 3730XL by Guangzhou Tianyi Huiyuan Gene Technology Co., Ltd. (Guangzhou, China). Chromatograms were assembled with Geneious 11.0.3. The assembled sequence was translated to amino acids using the invertebrate mitochondrial code to check for stop codons and frame shifts and was compared via BLAST against the GenBank database to check for contamination and pseudogenes (e.g., nuclear mitochondrial DNA, NUMT) as implemented in Geneious 11.0.3. The sequences generated from this study are deposited in GenBank (accession numbers are shown in Suppl. material 1).

Phylogenetic analysis

Multiple sequence alignments for each gene were performed with MAFFT v7.490 (Katoh and Standley 2013) by the E-INS-i strategy for 18S and 28S, and the L-INS-i strategy for COI and wingless. Maximum likelihood phylogenetic analyses were conducted in IQ-TREE (v. 2.1.3) (Minh et al. 2020) following the methodology of Chen et al. (2021). Eight partitions were specified in the original concatenated alignment: one for each ribosomal gene and three for each codon position in COI and wingless (Chernomor et al. 2016). ModelFinder was employed to determine the best nucleotide substitution model for each partition and to merge partitions to increase overall model fit (Kalyaanamoorthy et al. 2017). Branch support was estimated with 1000 ultrafast bootstrap replicates (Hoang et al. 2018). Ten independent tree searches were conducted, and we present the tree with the greatest log-likelihood score. *Maruzza japonica* Mineo was selected as the outgroup.

Table 1. Primer pairs used in this study.

Gene	Primer name	Primer sequence 5' to 3'	Reference
18S	ai	CCTGAGAAACGGCTACCACATC	Whiting et al. (1997)
18S	18S-5R	CTTGGCAAATGCTTTCGC	Giribet et al. (1996)
28S	D23F	GAGAGTTCAAGAGTACGTG	Whiting et al. (1997)
28S	28Sb	TCGGAAGGAACCAGCTACTA	Whiting et al. (1997)
COI	HCO-2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
COI	LCO-1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
Wingless	SceWgIF-1	GTAAGTGTCACGGGATGTC	Chen et al. (2021)
Wingless	SceWgIR-1	TTGACTTCACAGCACCAGT	Chen et al. (2021)

Imaging

Photographs of live specimens were taken with a Canon 5D Mark III (Tokyo, Japan) camera with a 100 mm macro lens. Multifocal images of mounted specimens were made using a Nikon SMZ25 microscope with a Nikon DS-Ri 2 digital camera system and a Macropod Microkit photography system. All image stacks were rendered using Helicon Focus. Scanning electron micrographs were produced using a Phenom Pro Desktop SEM. Images were post-processed with Adobe Photoshop CS6 Extended.

Results

The phylogenetic analysis retrieved *Trissolcus siliangae* Yan, Chen & Talamas sp. nov. embedded within *Trissolcus*, as the sister taxon to a clade comprising (*T. vindicius* + *T. cultratus*) + (*T. corai* + (*T. japonicus* + *T. plautiae*)) (Fig. 6).

Treatment of *Protelenomus* as a derived lineage of *Trissolcus* is also supported by a morphological character, the subacropleural sulcus. Talamas et al. (2017) proposed that this sulcus had value for circumscribing *Trissolcus* and noted that it was present in all Palearctic *Trissolcus* except for *T. exerrandus* Kozlov & Lê. Notably, a preliminary phylogenetic analysis indicates that *T. exerrandus* does not belong in *Trissolcus*, although its destination is presently unclear. In their synonymy of *Latonius* Kononova, Vasiliţa et al. (2021) reported that *T. planus* (Kononova) does not have a subacropleural sulcus. In the figures provided in the revision of *Protelenomus* by Veenakumari et al. (2019), the subacropleural sulcus is present in *T. anoplocnemidis* (Ghesquière), *T. gajadanta* (Veenakumari), *T. maasai* (Veenakumari), *T. tibialis* (Veenakumari), and *T. zulu* (Veenakumari), whereas it is clearly absent in *T. flavicornis* (Kieffer). This character can be difficult to assess in species with coarse sculpture and from images with glare on the specimens. In *T. siliangae* sp. nov., the subacropleural sulcus is clearly visible in Figs 3F and 4B. Given that this sulcus appears to be absent in some highly derived species, we consider that it may still be a synapomorphy for

the genus, albeit with secondary losses. The subacropleural sulcus thus remains useful for affirming placement in *Trissolcus*, but its absence cannot be used to exclude species from the genus.

Synonymy

Trissolcus Ashmead

Trissolcus Ashmead, 1893: 161 (original description. Type: *Telenomus brochymenae* Ashmead, by original designation. Key to species).

Asolcus Nakagawa, 1900: 17 (original description. Type: *Asolcus nigripedius* Nakagawa, by monotypy. Synonymized with *Trissolcus* by Masner (1964)).

Protelenomus Kieffer syn. nov., 1906: 6 (original description. Type: *Protelenomus flavicornis* Kieffer, by monotypy).

Aphanurus Kieffer, 1912: 10, 69 (original description. Type: *Teleas semistriatus* Nees von Esenbeck, by original designation. Preoccupied by *Aphanurus* Looss (1907) (Trematoda).

Immsia Cameron, 1912: 104 (original description. Type: *Immsia carinifrons* Cameron, by monotypy. Synonymized with *Microphanurus* Kieffer by Nixon (1938)).

Microphanurus Kieffer: Kieffer 1926: 16, 91 (replacement name for *Aphanurus* Kieffer. Type: *Teleas semistriatus* Nees von Esenbeck, by substitution of *Microphanurus* for *Aphanurus*. Description, keyed, key to species. Synonymized with *Asolcus* Nakagawa by Watanabe (1951)).

Epinomus Ghesquière, 1948: 324 (original description. Type: *Epinomus anoplocnemidis* Ghesquière, by monotypy and original designation. Synonymized with *Protelenomus* by Masner (1976)).

Latonius Kononova, 1982: 76 (original description. Type: *Latonius planus* Kononova, by monotypy and original designation. Synonymized with *Trissolcus* by Vasiliţa et al. (2021)).

Kozlotelenomus Mineo, O'Connor & Ashe, 2009: 193 (original description. Type: *mopsus* Nixon, by monotypy and original designation. Synonymized with *Trissolcus* by Talamas and Buffington (2015)).

Ioseppinella Mineo, O'Connor & Ashe, 2010: 267 (original description. Type species *Ioseppinella serena* Mineo, O'Connor & Ashe, by monotypy and original designation. Synonymized with *Trissolcus* by Vasiliţa et al. (2021)).

Generic transfers

Trissolcus anoplocnemidis (Ghesquière), comb. nov.

Epinomus anoplocnemidis Ghesquière, 1948: 325 (original description); Risbec 1950: 568, 576 (description, keyed).

Protelenomus anoplocnemidis (Ghesquière): Masner 1976: 77 (generic transfer); Johnson 1992: 565 (cataloged, type information); Rajmohana 2013: 3 (description); Veenakumari et al. 2019: 384, 389 (diagnosis, keyed).

***Trissolcus areolatus* (Rajmohana), comb. nov.**

Protelenomus areolatus Rajmohana, 2013: 2 (original description, diagnosis); Veenakumari et al. 2019: 384 (keyed).

***Trissolcus flavicornis* (Kieffer), comb. nov.**

Protelenomus flavicornis Kieffer, 1906: 7 (original description); Kieffer 1926: 22 (description); Bin 1974: 458 (type information); Johnson 1992: 565 (cataloged, type information); Veenakumari and Mohanraj 2015: 306 (description, new distribution record for India); Veenakumari et al. 2019: 384, 389 (description, diagnosis, keyed).

***Trissolcus gajadanta* (Veenakumari), comb. nov.**

Protelenomus gajadanta Veenakumari, 2019: 384 (original description, keyed)

***Trissolcus lutuli* (Veenakumari), comb. nov.**

Protelenomus lutuli Veenakumari, 2019: 384, 385 (original description, keyed)

***Trissolcus maasai* (Veenakumari), comb. nov.**

Protelenomus maasai Veenakumari, 2019: 384, 386 (original description, keyed)

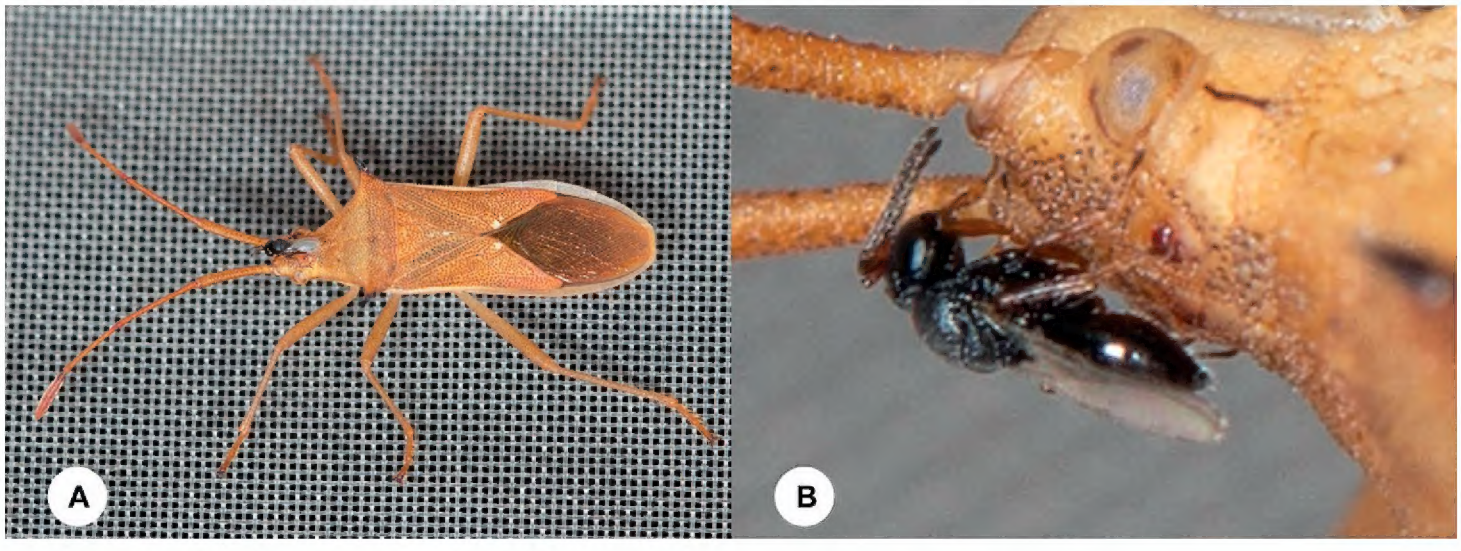

Figure 1. A female *Trissolcus siliangae* on *Cletus punctiger* **B** closeup of *T. siliangae* on *C. punctiger* from Fig. 1A.

***Trissolcus tibialis* (Veenakumari), comb. nov.**

Protelenomus tibialis Veenakumari, 2019: 384, 387 (original description, keyed)

***Trissolcus yao* (Veenakumari), comb. nov.**

Protelenomus yao Veenakumari, 2019: 384, 388 (original description, keyed)

***Trissolcus zulu* (Veenakumari), comb. nov.**

Protelenomus zulu Veenakumari, 2019: 384, 388 (original description, keyed)

Species description

***Trissolcus siliangae* Yan, Chen & Talamas, sp. nov.**
https://zoobank.org/DAD99C7C-D538-43D9-A43B-577A27D1C9B3
Figs 1–4

Description. Female body length: 1.28 mm (n = 4). Body color: head, mesosoma, and metasoma black, shining. Mandible color: red-brown. Leg color: coxae and tarsi dark brown, rest of legs yellow-brown. Tegulae yellow-brown. Antennal color: radicle and A1–A2 yellow to brown, darker dorsally; A3–A11 dark brown.

Head. Length of radicle: less than width of clypeus. Claval formula: A8–A11:1-1-1-1. Facial striae: present. Number of clypeal setae: 4. Shape of gena in lateral view: moderately wide, bulging. Genal carina: absent. Malar striae: absent. Sculpture of malar sulcus: smooth. Orbital furrow: expanded at intersection with malar sulcus, medial margin of furrow poorly defined. Macrosculpture of frons directly dorsal to the antennal scrobe: absent. Preocellar pit: absent. Setation of lateral frons: sparse. Punctation of lateral frons: absent. Sculpture directly ventral to preocellar pit: coriaceous microsculpture. Rugae on lateral frons: absent. OOL: about one ocellar diameter. Hyperoccipital carina: absent. Macrosculpture of posterior vertex: absent. Microsculpture on posterior vertex along occipital carina: coriaceous. Anterior margin of occipital carina: crenulate. Medial part of occipital carina in dorsal view: rounded.

Mesosoma. Epomial carina: present. Macrosculpture of lateral pronotum directly anterior to netrion: finely rugulose. Netrion sulcus: incomplete, only weakly defined ventrally. Pronotal suprahumeral sulcus in posterior half of pronotum: absent. Number of episternal foveae: 2. Course of episternal foveae ventrally: abutting dorsal apex of acetabular carina. Course of episternal foveae dorsally: distinctly separate from mesopleural pit. Subacropleural sulcus: present. Speculum: transversely strigose. Mesopleural pit: simple. Mesopleural carina: absent. Sculpture of femoral depression: smooth. Patch of striae at posteroventral end of femoral depression: present, striae orthogonal to long axis of femoral depression. Setal patch at posteroventral end of femoral depression:

present as a line of setae. Microsculpture of anteroventral mesopleuron: present in anterior portion, smooth posteriorly. Macrosculpture of anteroventral mesopleuron: absent. Postacetabular sulcus: present as a smooth furrow. Mesopleural epicoxal sulcus: indicated by shallow foveae. Setation of posteroventral metapleuron: absent. Sculpture of dorsal metapleural area: rugulose. Posterodorsal metapleural sulcus: undifferentiated. Paracoxal sulcus in ventral half of metapleuron: absent. Length of anteroventral extension of metapleuron: short, not reaching base of mesocoxa. Metapleural epicoxal sulcus: indistinguishable from rugose sculpture. Mesoscutal humeral sulcus: comprised of shallow foveae. Median mesoscutal carina: absent. Microsculpture of mesoscutum: coriaceous. Mesoscutal suprahumeral sulcus: comprised of shallow foveae. Length of mesoscutal suprahumeral sulcus: about two-thirds the length of anterolateral edge of mesoscutum. Parapsidal line: present. Notaulus: absent. Median protuberance on anterior margin of mesoscutellum: absent. Shape of dorsal margin of anterior lobe of axillar crescent: flat. Sculpture of anterior lobe of axillar crescent: dorsoventrally strigose. Area bound by axillar crescent: smooth. Macrosculpture of mesoscutellum: absent. Microsculpture on mesoscutellum: coriaceous. Median mesoscutellar carina: absent. Setation of posterior scutellar sulcus: absent. Form of metascutellum: broad, short, rugose projection. Metanotal trough: foveate, foveae occupying less than half of metanotal height. Metapostnotum: invaginated laterally, propodeum and metanotum directly adjacent. Anteromedial portion of metasomal depression: rugulose.

Wings. Length of postmarginal vein: about twice as long as stigmal vein. Fore wing apex: reaching beyond T6.

Legs. Color: coxae and distal tarsomeres dark brown to black, otherwise yellow to light brown. Anteroventral area of hind femora: not covered by setae. Femur and tibia not enlarged. Basitarsi of fore leg with a row of densely stout bristles at basal half. Claws well developed, curved.

Metasoma. Width of metasoma: about equal to width of mesosoma. Longitudinal striae on T1 posterior to basal costae: present. Number of sublateral setae (on one side): 0. Setation of laterotergite 1: absent. Striation on T2: extending about half the length of the tergite, weakly indicated. Setation of T2: present along lateral margin. Setation of laterotergite 2: present. Striation on S2 striate: present laterally, length of striae extending up to anterior half, remainder smooth. S2 felt fields: present. Sculpture of S3–S6: setigerous punctate.

Male. Unknown.

Diagnosis. Moniliform antennae in females are rare in Scelionidae, shared in *Trissolcus* by *T. siliangae*, *T. flavicornis*, *T. gajadanta*, and *T. planus*; these species also have a single papillary sensillum on each clavomere. Care should be taken to count the antennomeres (11 in females, 12 in males) so that female specimens are not mistaken for males. Clavomeres that are only slightly wider than the preceding flagellomeres are more common, found in many species of the former *Protelenomus* and in more typical *Trissolcus* such as *T. sipioides*.

Trissolcus siliangae has a laterally invaginated metapostnotum, as in *T. hullensis* (Johnson 1985), which is found in a minority of *Trissolcus* species. In Veenakumari et

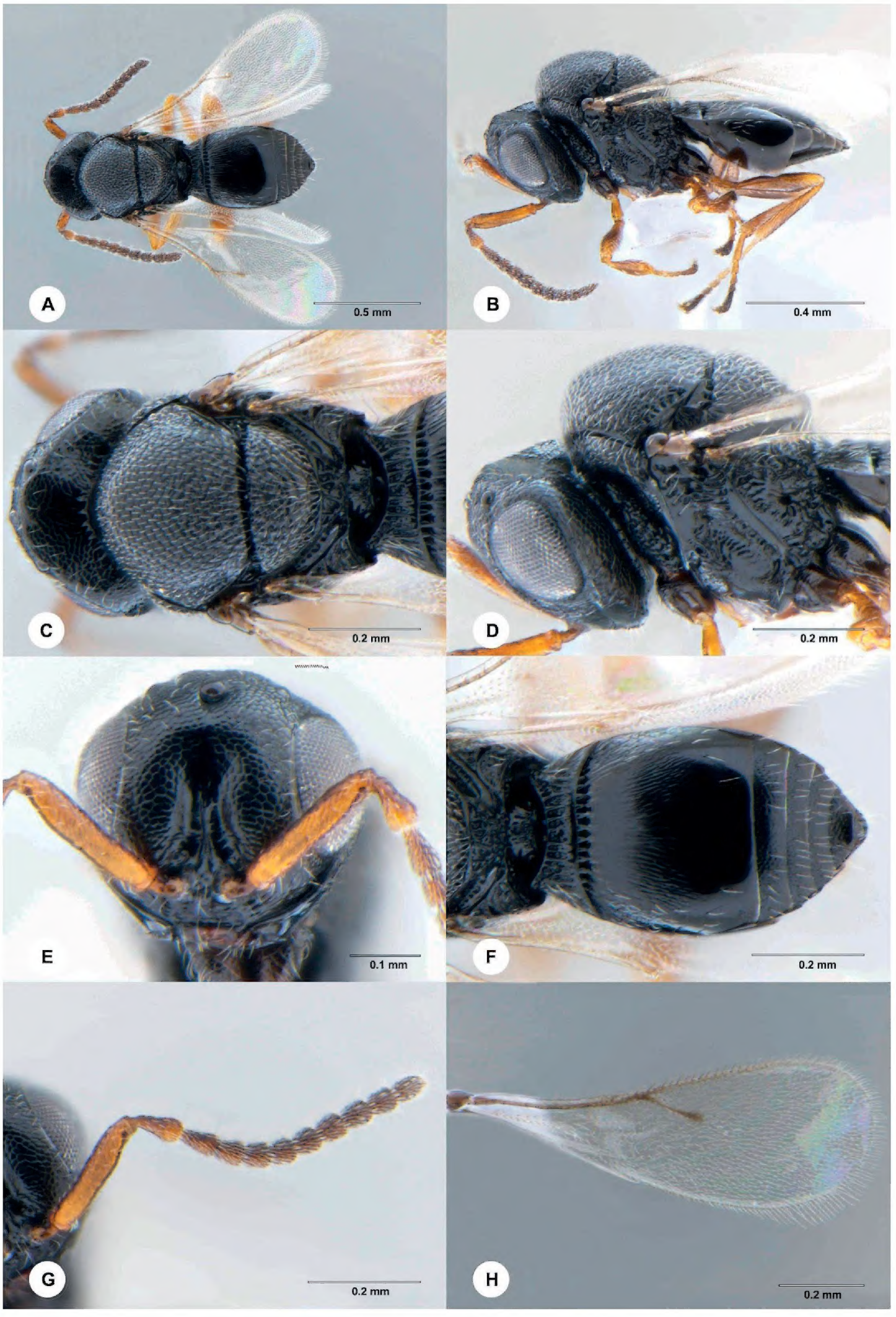

Figure 2. *Trissolcus siliangae*, paratype, female (SCAU 3042799) **A** dorsal habitus **B** lateral habitus **C** head and mesosoma, dorsal view **D** head and mesosoma, lateral view **E** head, anterior view **F** metasoma, dorsal view **G** antenna **H** fore wing.

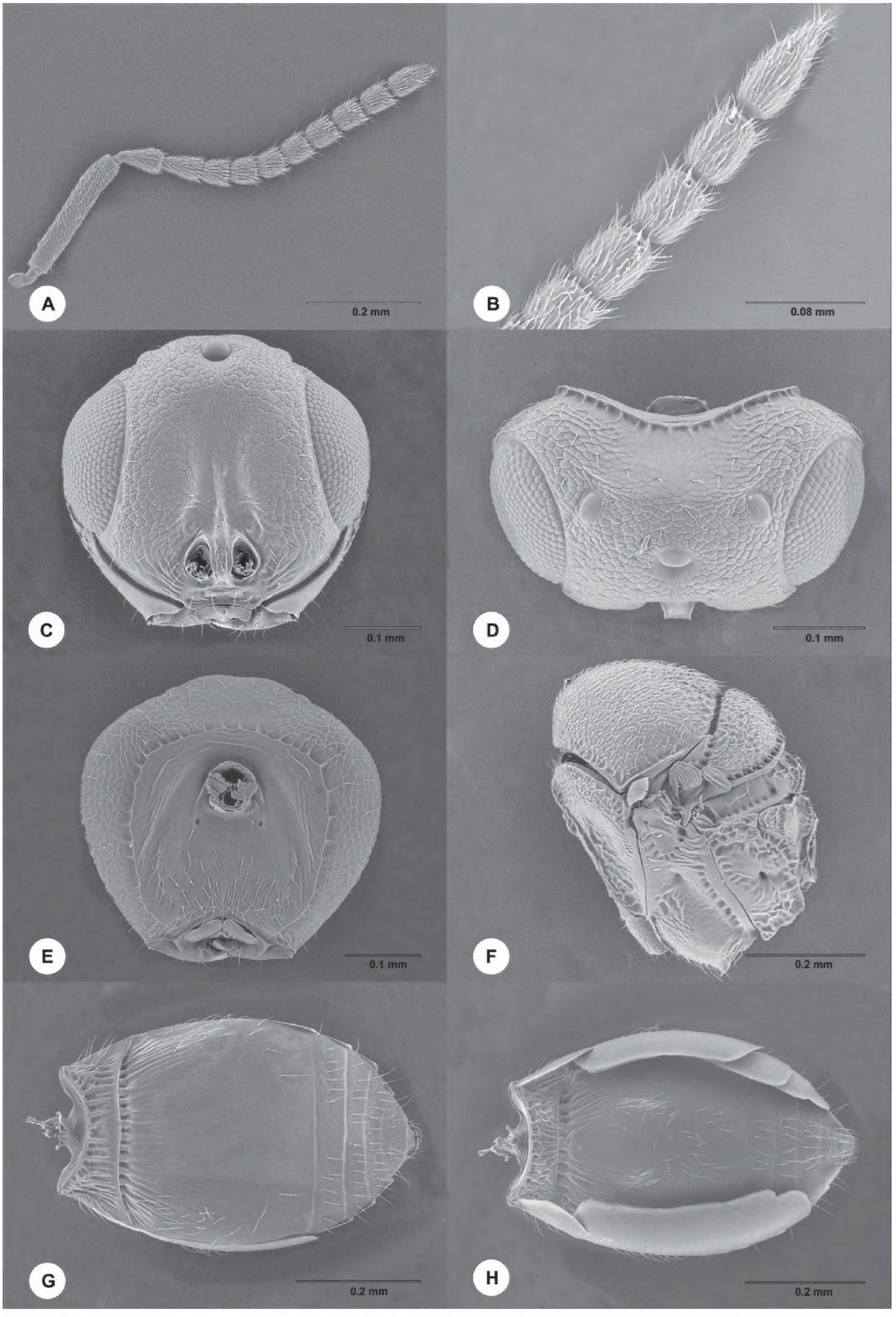

Figure 3. *Trissolcus siliangae*, paratype, female (SCAU 3042799) **A** antenna **B** apical antennal segments **A** head, anterior view **D** head, dorsal view **E** head, ventral view **F** mesosoma, lateral view **G** metasoma, dorsal view **H** metasoma, ventral view.

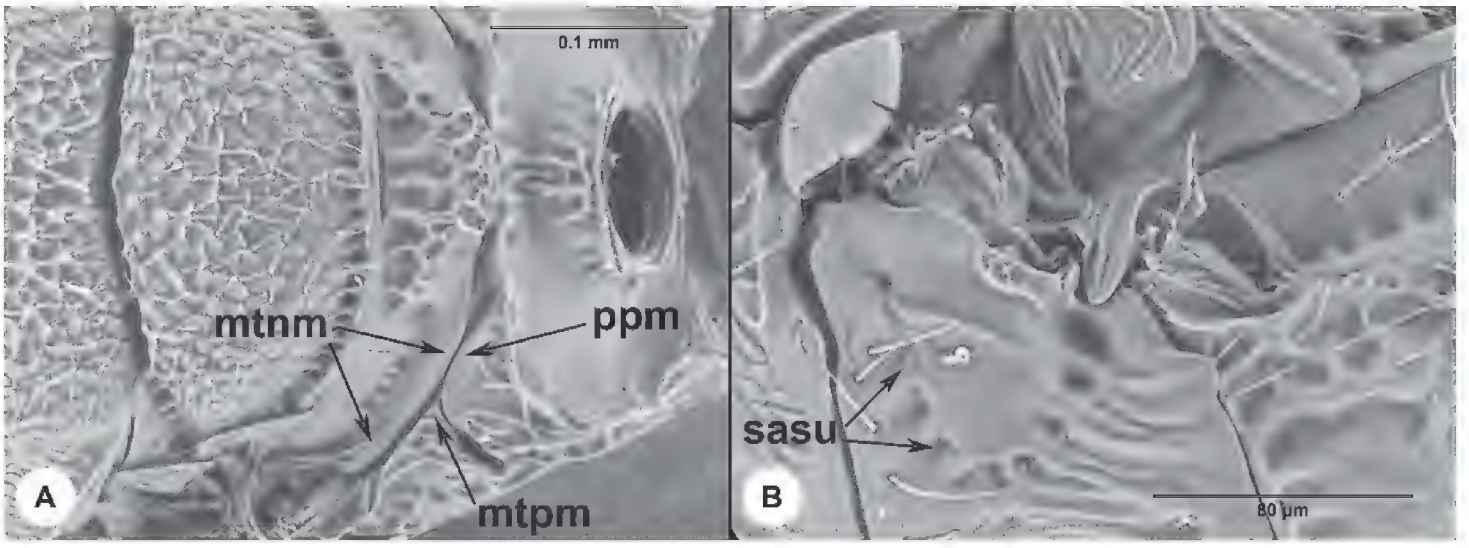

Figure 4. *Trissolcus siliangae*, paratype, female (SCAU 3042799) **A** mesosoma, dorsal view **B** dorsal mesopleuron, lateral view.

al. (2019), the metapostnotum in *T. flavicornis* appears to extend medially, separating the propodeum from the metanotum until it reaches the vicinity of the lateral margin of the metascutellum (see figures 27, 29, and 31 of that publication). We find this to be the case for *T. gajadanta* as well, based on examination of a specimen from Ivory Coast (Fig. 5). *Trissolcus siliangae* can thus be separated by the combination of the moniliform antennae, claval formula (1-1-1-1), and lateral invagination of the metapostnotum. Additionally, *T. siliangae* can be separated from the very similar *T. gajadanta* by the striation on T2: robust in the anterior ⅔ of the tergite in *T. gajadanta* and only weakly present in *T. siliangae*; and by the robust parapsidal lines in *T. gajadanta*, which are not indicated in *T. siliangae*. Notably, the posterior head in *T. gajadanta* has two concavities lateral to a dorsoventral median ridge, with the dorsal part of the occipital carina located low on the posterior head (Fig. 5B).

Etymology. This species is named after one of its collectors, Dr. Siliang Wang, for her discovery of this species.

Material examined. ***Holotype***, female: **China:** Zhejiang, Wenzhou, corn field, 27.609301°N, 120.508985°E, phoretic on *Cletus punctiger* Dallas, 10.IX.2021, Cheng-jin Yan, SCAU 3042644 (deposited in SCBG). ***Paratypes*:** (3 females) **China:** 2 females, same data as holotype, SCAU 3042799, 3041198 (SCBG); 1 female, **China:** Zhejiang, Wenzhou, corn field, 27.609301°N, 120.508985°E, phoretic on *Cletus punctiger* Dallas, 10.IX.2021, Siliang Wang, SCAU 3044000 (WVCST).

Distribution. China (Zhejiang).

Discussion

The phenomenon of phoresy has been documented in a variety of scelionids: *Paratelenomus anu* Rajmohana, Sachin & Talamas (Rajmohana et al. 2019), *Thoronella* Masner (Carlow 1992), *Synoditella* Muesebeck (Lanham and Evans 1958), *Sceliocerdo* Muesebeck (Brues 1917), *Scelio* Latreille (Ramachandra Rao

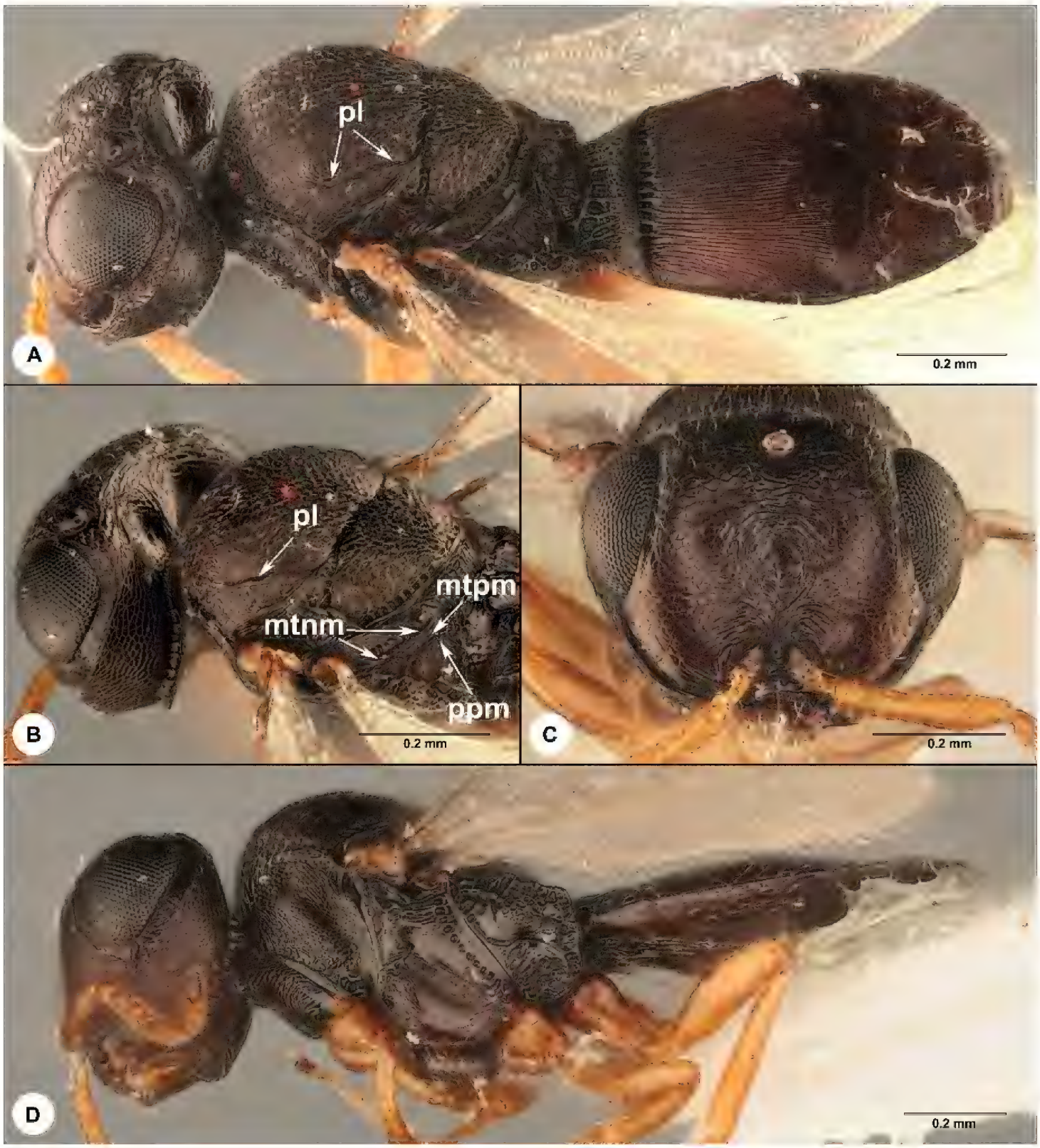

Figure 5. *Trissolcus gajadanta*, female (OSUC 398371) **A** head, mesosoma, metasoma, dorsolateral view **B** head and mesosoma, posterolateral view **C** head, anterior view **D** head, mesosoma, metasoma, lateral view.

1952), *Mantibaria* Kirby (Maglić and Žikić 2021), *Telenomus* (Orr et al. 1986; Arakaki et al. 1995), and *Trissolcus*. These taxa are distantly related within Scelionidae and present examples of evolutionary convergence. Phoresy occurs in *Trissolcus*, *Paratelenomus*, and some *Telenomus* that parasitize heteropteran eggs and are part of a scelionid radiation on Hemiptera (Chen et al. 2021). The scelionids not associated with Hemiptera are more distantly related and they also attack more distantly related hosts: Orthoptera, Mantodea, Lepidoptera, and Odonata, although it should be noted that phoretic parasitoids of Lepidoptera can be found within *Telenomus* (Arakaki et al. 1995). Detailed examination of this assortment of relationships may

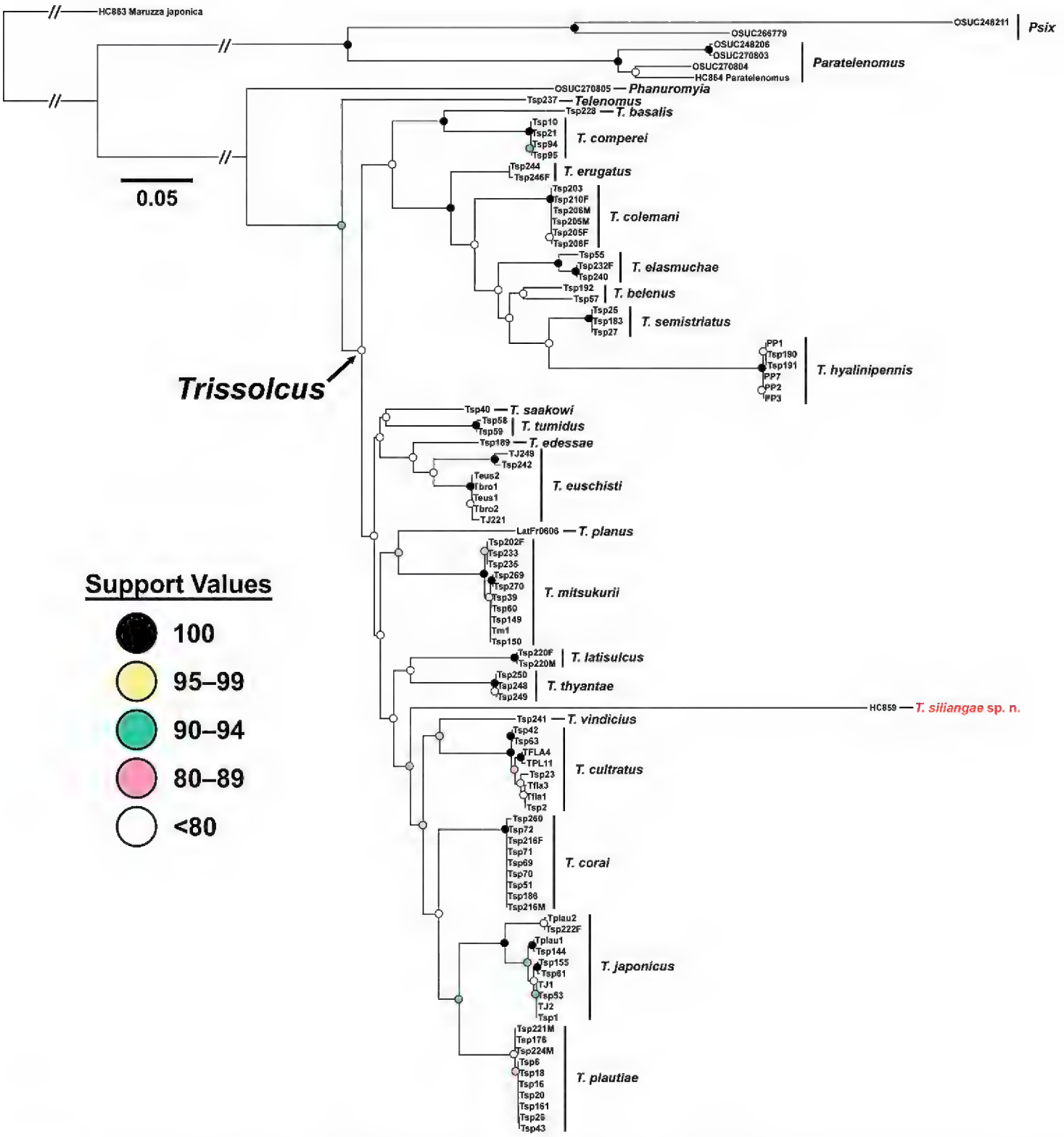

Figure 6. Four-gene maximum likelihood phylogenetic analysis of a modified dataset of Talamas et al. (2019) and Vasiliţa et al. (2021). Scale bar in the expected number of nucleotide substitutions per site. Ultrafast bootstrap support values indicated by colored circles at nodes. Some nodes were not annotated due to short branch lengths.

yield information on the selection pressures for phoresy, which may include finding the eggs or reaching the eggs at a stage sufficiently early for parasitoid development to occur, or to have a competitive advantage. In *Trissolcus*, interspecific competition is common, and being the first parasitoid may yield an advantage for intrinsic (larval) competition. Phoresy in *Trissolcus* is worth further examination, both in terms of behavioral studies that will illuminate its benefits, and further phylogenetic analysis to determine if it has evolved more than once in the genus, and to identify sister taxa to phoretic lineages.

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Supplementary material 1

Sequenced taxa and GenBank accession numbers

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Data type: table

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